11 Insects and Climate Change: Processes, Patterns and Implications for Conservation

Robert J. Wilson,[1] Zoe G. Davies[2] and Chris D. Thomas[3]

[1]*Área de Biodiversidad y Conservación, Escuela Superior de Ciencias Experimentales y Tecnología, Universidad Rey Juan Carlos, Tulipán s/n, Móstoles, E-28933 Madrid, Spain;* [2]*Centre for Evidence-Based Conservation, School of Biosciences, University of Birmingham, Edgbaston, Birmingham B15 2TT, UK;* [3]*Department of Biology (Area 18), University of York, PO Box 373, York YO10 5YW, UK*

1 Introduction

The effects of climate change on biodiversity represent one of the most pressing challenges for conservationists in the 21st century. Although the great diversity of life has evolved and survived alongside continual climatic variation, the ability of biodiversity to respond to contemporary climate change is much more of an unknown, given the potentially unprecedented rate and magnitude of projected increases in the earth's surface temperature (IPCC, 2001; Root and Schneider, 2002; King, 2005; Lovejoy and Hannah, 2005). In the distant past, at least some of the comparable increases in temperature probably triggered mass extinction events (Hallam and Wignall, 1997; Benton and Twitchett, 2003). Coupled with the fact that many species are now restricted to very small areas of occupancy because of direct habitat loss and fragmentation caused by human activity (Vitousek *et al*., 1997; Sanderson *et al*., 2002; Gaston *et al*., 2003), the stresses imposed by climate change on habitats, life histories and interactions between species may be such that widespread extinctions are inevitable unless climate change can be arrested or effective conservation measures can be adopted (Thomas, C.D. *et al*., 2004).

Recent reviews and meta-analyses show that a wide variety of ecological systems and taxa are already changing in ways consistent with climate change (Hughes, 2000; Walther *et al*., 2002; Parmesan and Yohe, 2003; Root *et al*., 2003), and many of the examples have been drawn from research conducted on insects. In this chapter we show how insect biodiversity is affected and potentially threatened, and the importance of insects as model systems for biological responses to climate change and associated conservation measures. We first present evidence of recent responses to climate change, concentrating on

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insect examples. We then examine evidence for the mechanisms behind those responses, before using an understanding of these mechanisms to address the likely future effects of climate change on insects, and the conservation actions that will be required to minimize negative effects on biodiversity. Global modelling of biogeographic responses to climate change suggests that there will be sweeping changes to local ecosystems and communities (Sala *et al*., 2000; Peterson *et al*., 2002), confirmed by palaeological and recent evidence that show the individualistic responses of species distributions to climate change (Thomas *et al*., 2001; Coope, 2004). In this chapter, we particularly ask how the life histories of individual insect species influence their vulnerability, and propose adaptive strategies to identify susceptible species and manage for their well-being.

2 Recent Responses to Climate Change

Biological systems respond to a wide range of environmental drivers, of which climate change is only one. Current declines in the global distributions, population sizes and genetic diversity of species are associated with anthropogenic processes such as habitat loss and fragmentation, pollution, overexploitation of natural resources and the spread of invasive alien species (Sala *et al*., 2000; Thomas, J.A. *et al*., 2004; Balmford and Bond, 2005). Given the effects of these alternative and interacting factors, the sensitivity of climate change as a political issue and positive bias towards the publication of significant results, an onus has been placed on scientists to identify an unequivocal role of climate change in driving biological changes. Meta-analyses of studies conducted for a wide variety of taxa and geographical regions have shown convincing evidence that biological systems are already changing in ways consistent with, and only satisfactorily explained by, climate change (Parmesan and Yohe, 2003; Root *et al*., 2003). The two best-documented climate-related biological changes are shifts in species distributions and changes in phenology, with species shifting their ranges to higher latitudes and elevations, and life cycles beginning earlier in spring and continuing later in autumn associated with increasing temperatures (Hughes, 2000; Walther *et al*., 2002). We now consider the evidence for these changes that has been provided by studies on insects.

2.1 Shifts in species distributions

The geographical ranges of most species have upper and lower latitudinal limits, and often have lower and upper elevational limits within particular regions (MacArthur, 1972; Gaston, 2003). These boundaries to geographic ranges are often set by regional climates that determine both the average availability of temperature, water and suitable conditions for growth and reproduction, and the most extreme conditions to which species and their essential biotic resources are exposed. As small, ectothermic organisms, insects are particularly sensitive to fluctuations in local temperature or moisture levels and, as a result, their distributions and habitat use are often closely related to climate.

For example, the northern range limits of British butterfly species are closely correlated with summer isotherms, reflecting the availability of warm conditions for development and adult activity at upper latitudinal range margins (Thomas, 1993). In addition, at increasing latitudes, butterflies become progressively more restricted to warm microhabitats characterized, for example, by south-facing slopes, short vegetation and bare ground, emphasizing the temperature limitation of species as they approach their 'cool', upper latitudinal margins (Thomas, 1993; Thomas *et al*., 1998, 1999). There is also strong evidence that summer heat availability sets upper latitudinal limits to the distributions of many species of Hemiptera in the Arctic and northern Europe (Strathdee *et al*., 1993; Hill and Hodkinson, 1995; Whittaker and Tribe, 1996; Miles *et al*., 1997; Judd and Hodkinson, 1998; Hodkinson *et al*., 1999). In contrast, insect distributions may be limited at their lower latitudinal margins by excessive temperatures or inadequate moisture availability, either directly through limits to their physiological tolerance or indirectly through climate effects on larval host plants in the case of herbivorous insects (Bale *et al*., 2002; Hawkins *et al*., 2003). Perhaps as a consequence of these two distinct patterns at 'cool' and 'warm' range margins, butterfly species richness in 220 × 220 km grid squares across Europe is closely correlated with actual evapotranspiration, a measure that takes into account both temperature and moisture availability. Species richness is greatest in warm, wet cells in central Europe, and declines both towards cool northern Europe and the hot dry Mediterranean, probably reflecting both declines in plant productivity and direct effects of temperature on insect physiology (Hawkins and Porter, 2003).

Given climatic limitation to species distributions, climate change is expected to shift the locations of suitable climates for species. Therefore, species distributions might expand into regions that become suitable and retract from regions that cease to be so. Recent climate warming is expected to cause range shifts to higher latitudes and elevations. The first documented example of such a range shift was provided by work on Edith's checkerspot butterfly *Euphydryas editha* (Parmesan, 1996, 2005), a non-migratory species that breeds in discrete localities in North America. By the 1990s, populations of *E. editha* had gone extinct from many locations, even though its larval host plants and apparently suitable habitat remained. Rates of local extinction were greatest at low latitudes and at low elevations, such that the average location of populations increased by 92 km northwards and 124 m upwards. In the same 100-year period mean annual isotherms moved 105 km northwards and 105 m upwards, suggesting a climatic link that is supported by the mechanisms involved in local extinctions in this species (Parmesan, 2005). Temperature and precipitation during spring determine: (i) whether *E. editha* adults emerge at a time when conditions are reliable for flight and reproduction (Singer and Thomas, 1996; Thomas *et al*., 1996); and (ii) whether larvae reach diapause before summer host plant senescence (Weiss *et al*., 1988). Drier, hotter and more extreme or unpredictable climatic conditions increase extinction risk at low latitudes and elevations (McLaughlin *et al*., 2002a,b), leading to a northward and upward shift in the average latitudes and elevations of populations.

One of the first multispecies studies of range changes associated with climate change also showed a predominant pattern of poleward shifts in butterfly distributions. Species ranges shifted northwards during the 20th century for 22 (63%) of 35 non-migratory European butterflies that had data for both northern and southern margins (Parmesan *et al*., 1999). Only two of the species showed southward shifts, and regional climate warming is the most likely explanation for the predominant pattern of colonization at upper latitudinal margins and/or extinction at lower latitudinal margins. For the species whose ranges shifted polewards, 21 (96%) showed northern range margin expansions and only 8 (36%) showed southern margin contractions. A larger sample of species that had data from at least one margin also showed a greater proportion of species with northern margin expansions (34 out of 52 species) than southern margin contractions (10 out of 40 species).

Following Parmesan *et al*. (1999), several studies have documented range expansions by butterflies beyond their former upper latitudinal margins (e.g. Hill *et al*., 1999b, 2001; Crozier, 2003, 2004a,b). Butterflies have been valuable model systems because of a wealth of historical data about their distributions, and because they depend on thermal conditions throughout their life cycles. Insects vary greatly in their habitat use, thermal physiology and dispersal capacity, but recent research suggests that the upper latitudinal margins of many other insect taxa have also shifted northwards in response to recent climate change (Hickling *et al*., 2005, 2006; Table 11.1). In this and other contexts, such as phenological change, large-scale and long-term monitoring schemes have provided invaluable evidence for the effects of climate change on a wide range of taxonomic groups (see Conrad *et al*., Chapter 9, this volume). Experimental studies suggest that the mechanisms involved in range expansions have been similar across insect taxa (Crozier, 2003, 2004a,b; Musolin and Numata, 2003; Karban and Strauss, 2004; Battisti *et al*., 2005, 2006; Table 11.1).

The relative paucity of evidence for contractions at warm, lower latitudinal margins is no cause for optimism about the fate of species where conditions are deteriorating. Range expansions are easier than contractions to detect because colonizations directly lead to species' presence in regions or large-scale grid cells, whereas local extinctions lead to the gradual decline of species to isolated populations within a region, which may be unlikely to persist in the long term (Wilson *et al*., 2004). Many species may be suffering declines at their warm margins that go undetected because their regional populations persist but shift to higher elevations. Two studies have shown recent increases in the average elevations of atlas grid cells occupied by butterfly species. In Britain, four butterfly species at the southern margins of their distributions have gone extinct from low-elevation 10 km grid cells and colonized high-elevation cells, leading to a mean increase in elevation of 41 m between pre-1970 and 1999 (Hill *et al*., 2002). In the Czech Republic, the average altitude of occupied atlas grid cells (~11 × 12 km) increased significantly for 15 butterfly species between 1950 and 2001, with 10 species retracting from low altitudes, 12 expanding at high altitudes and a mean upward shift of 60 m (Konvicka *et al*., 2003). Actual recent changes in species' elevational ranges may be even greater than recorded in studies based on grid cells, since such cells may include wide altitudinal variation, particularly in mountainous regions. For example, in the study of Czech butterfly distributions, mean elevational range

Table 11.1. Examples of evidence for recent climate-related distributional shifts in insect species.

Evidence for climate-related range shift	Taxa (Location)	References
(a) Multispecies correlational studies in warming climates		
Poleward latitudinal shifts: expansions at upper margins; contractions at lower margins; increase in average latitude.	Butterflies (Europe)	Parmesan *et al*. (1999)
	Odonata, Orthoptera, Hemiptera, Lepidoptera, Coleoptera (Britain)	Hickling *et al*. (2005, 2006)
Upward elevational shifts: colonizations at upper margins; extinctions at lower margins; increase in average altitude.	Butterflies (Britain; Czech Republic; Spain)	Hill *et al*. (2002); Konvicka *et al*. (2003); Wilson *et al*. (2005); Franco *et al*. (2006)
	Odonata, Orthoptera, Hemiptera, Coleoptera (Britain)	Hickling *et al*. (2006)
(b) Mechanistic studies		
Extinctions at low elevations/ latitudes linked to rainfall decline and temperature increase; shift poleward (mean + 92 km) and upward (mean + 124 m).	Butterfly *Euphydryas editha* (Western North America)	Parmesan (1996, 2005) (See also McLaughlin *et al., 2*002a,b; Thomas, 2005)
Extension of upper latitudinal margin linked to increased overwintering survival at warmer temperatures.	Bug *Nezara viridula* (Japan)	Musolin and Numata (2003)
Extension of upper latitudinal margin linked to warmer temperatures and higher humidity, increasing egg hatch and population size.	Bug *Philaenus spumarius* (California)	Karban and Strauss (2004)
Extension of upper latitudinal margin linked to increased overwintering survival at warmer temperatures; possible role of increased growth rate and voltinism in warmer summers.	Butterfly *Atalopedes campestris* (Pacific Northwest, USA)	Crozier (2003, 2004a,b)
Extension of upper latitudinal margin (+87 km) and upper elevational margin (+110–230 m) linked to: (i) increased winter larval survival; and (ii) increased summer adult dispersal at warmer temperatures.	Moth *Thaumetopoea pityocampa* (France, Italy)	Battisti *et al*. (2005, 2006)
Extension of habitat range linked to microclimate warming, resulting in increased habitat availability and habitat connectivity, permitting range expansion.	Butterfly *Hesperia comma* (Britain)	Thomas *et al*. (2001); Davies *et al*. (2005, 2006)

per cell was 250 m (Konvicka *et al*., 2003). However, it is difficult to attribute these uphill range shifts solely to the effects of climate change, because habitat degradation is typically more severe at lower elevations.

Sampling discrete locations in different time periods has the potential to detect elevational shifts at a finer resolution and to control the effects of habitat degradation. Research on the elevational associations of butterflies in the Sierra de Guadarrama (a mountain range in central Spain) showed that the lower elevational limits of 16 species that were restricted to high altitudes (i.e. species at their warm range margins) rose on average by 212 m (± SE 60), accompanying a 1.3°C rise (equivalent to 225 m) in regional mean annual temperature between 1967–1973 and 2004 (e.g. Fig. 11.1a and b) (Wilson *et al*.,

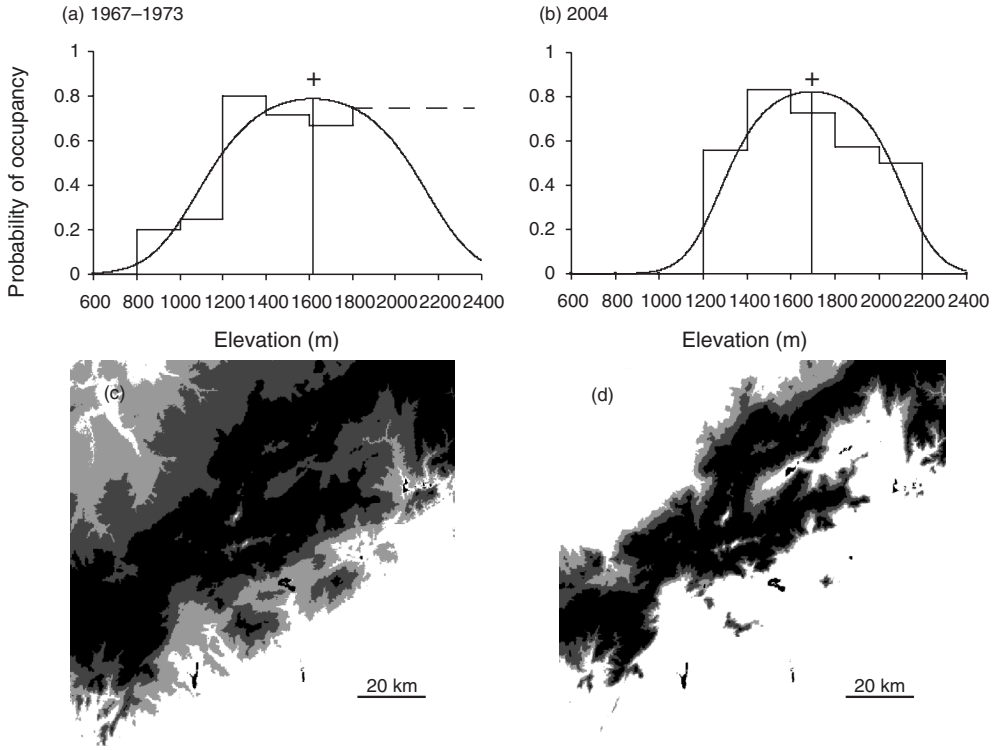

Fig. 11.1. Elevational associations of the butterfly *Lycaena alciphron* in the Sierra de Guadarrama (central Spain) in 1967–1973 and 2004. (a–b) Histograms of probability of occupancy in 200 m intervals (bars), and probability of occupancy modelled using logistic regression (curve) in (a) 1967–1973 and (b) 2004. Crosses show 'optimum' elevations with highest modelled probability of occupancy. In (a), dashed line denotes proportion of all four sites sampled above 1800 m. (c–d) Distributions of suitable elevations based on logistic regression models from (a) and (b), for (c) 1967–1973 and (d) 2004. Black: ≥50% probability of occupancy; dark grey: ≥20%; pale grey: ≥10%; white: <10%. For *L. alciphron*, optimum elevation increased from 1615 to 1694 m; lower elevational limit increased from 920 to 1320 m; and the area of suitable habitat (≥50% probability of occupancy) decreased by 38% between the surveys. (See Wilson *et al*., 2005.)

2005). The close correlation between temperature increase and changes in lower elevational limits, coupled with the fact that the larval host plants of the study species were widespread in the region (and that widespread butterflies which used the same larval host plants showed no elevational range shifts), implied that climate rather than direct habitat change was the most important driver in the system. For these species, increases in upper elevational limits were non-significant between the two surveys, probably because many species already occupied high altitudes in the region during the first time period. As a result, there were overall reductions in the elevational ranges of the species and an average decline of 22% in the 'climatically suitable' area for each species over only 30 years (e.g. Fig. 11.1c and d). These rapid declines in distribution size show how elevational shifts at lower latitudinal range margins can mask range contractions, constraining species distributions to progressively smaller areas until they may face regional extinction.

Relatively fine resolution (1 × 1 km) surveys in 2004/05 of the four northern/montane butterfly species in Britain have also detected higher levels of retreat since 1970 (Franco *et al*., 2006). Of the four species, *Erebia epiphron* retreated uphill by 130–150 m and showed no effects of habitat loss on its distribution; *E. aethiops* and *Aricia artaxerxes* retreated northwards by 70–100 km and showed combined impacts of climate change and habitat loss; and *Coenonympha tullia* declined through habitat loss, but showed no latitudinal or elevational shift. Averaged across the four species, it appears that climate change and habitat decline have been equally responsible for local extinctions near their range margins (Franco *et al*., 2006).

2.2 Shifts in phenology

In addition to the shift in space of species distributions, recent climate change has led to an ecological shift in time, with changes to the seasonality of species' life cycles (phenology). Phenological studies have predominantly shown species becoming active, migrating or reproducing earlier in the year, associated with increases in temperatures that lead directly to increased growth rates or earlier emergence from winter inactivity (Menzel and Fabian, 1999; Roy and Sparks, 2000; Fitter and Fitter, 2002; Peñuelas *et al*., 2002; Sparks and Menzel, 2002). Recent reviews of such studies show mean advances in the timing of spring events by 2.3–5.1 days per decade (Parmesan and Yohe, 2003; Root *et al*., 2003), depending on the type of analysis and range of examples included. Increasing temperatures have also allowed a number of species to remain active for a longer period during the year (Sparks and Menzel, 2002) or to increase their annual number of generations (Roy and Sparks, 2000).

Long-term data from several insect-recording schemes in Europe and North America have provided evidence for advancement in appearance dates of adult insects as annual temperatures have increased (Table 11.2). In Britain, the annual first appearance dates from 1976 to 1998 for 28 out of 33 butterfly species were negatively related to temperature for at least 1 month of the year (i.e. earlier appearance at higher temperatures), and an

increase in temperature of 1°C led to an average advance in first flight date of 4.5 days (Roy and Sparks, 2000). Conditions during early spring seem to be particularly important, with 22 species appearing significantly earlier associated with high February temperatures. The appearance dates of 11 species became significantly earlier in more recent years, even when taking account of monthly temperatures, suggesting either a progressive effect of some additional climatic or host plant effect or an evolutionary change. First appearance by butterflies has also advanced in California (North America) and Catalonia (Spain) associated with higher temperatures and lower rainfall in winter or spring (Forister and Shapiro, 2003; Stefanescu *et al*., 2003). There is a similar negative relationship between temperature and insect appearance dates in Austria, with three butterfly species, the bee *Apis mellifera* and the cockchafer *Melolonthus melolonthus* showing 3- to 5-day advances associated with 1°C warmer February–April temperatures (Scheifinger *et al*., 2005). However, in this case there was no temporal trend for earlier emergence, perhaps because population sizes of the species declined over time, leading to later first observations.

Mean flight dates (the estimated date of peak abundance during the adult flight period) for the first annual generations of species have advanced in conjunction with advances in first appearance date. For example, the peak of the

Table 11.2. Changes in annual appearance dates of insects associated with climate change.

Taxon	Location	Time period	Temperature increase	Change in appearance date	References
Butterflies	Britain	1976–1998	1.5°C (Feb–Apr mean); 1°C (May–July mean)	Advance, 26/35 spp. (13 significant, mean 8 days per decade)	Roy and Sparks (2000)
Butterfly (*Pieris rapae*)	NE Spain	1952–2000	1.4°C (annual mean)	Advance, 11.4 days	Peñuelas *et al*. (2002)
Butterflies	NE Spain	1988–2002	1–1.5°C (Feb, Mar, June mean)	Advance, 17/17 spp. (5 significant, mean 4.1 weeks)	Stefanescu *et al*. (2003)
Butterflies	California	1972–2002	1.2°C (annual daily max.)	Advance, 16/23 spp. (4 significant, mean 24 days)	Forister and Shapiro (2003)
Bee (*Apis mellifera*); Butterflies (*Aglais urticae*, *P. rapae*, *Gonepteryx rhamni*)	Austria	1951–1998	1.3°C (Feb–Apr mean)	Delay, 3–7 days	Scheifinger *et al*. (2005)

first generation of 104 common microlepidopteran species in the Netherlands advanced on average by 11.6 days between 1975 and 1994, accompanying a 0.9°C increase in annual mean temperature (Ellis *et al*., 1997; Kuchlein and Ellis, 1997). In Catalonian butterflies, changes in mean flight date advanced between 1988 and 2002 for 16 out of 18 species, with an average advance of 2.5 weeks for the 8 species with significant relationships (Stefanescu *et al*., 2003). In British butterflies, mean flight dates did not advance as much as first appearance dates, perhaps partly because mean flight date is affected by the number of generations that species have each year (Roy and Sparks, 2000). In univoltine species, mean flight date is closely correlated with first appearance date, but multivoltine species may increase their number of generations following early first emergence. For British butterflies, a trend in earlier first appearance was accompanied by a longer annual flight period in 24 species (overall average + 3 days per decade; n = 35 species), but this increase was particularly pronounced in several multivoltine species that were able to increase their number of generations in some parts of their range. For example, increases in average flight period of 8.9 days per decade for speckled wood *Pararge aegeria* and 13.1 days for comma *Polygonia c-album* reflect increased numbers of generations at higher latitudes.

Changes in insect phenology with year-to-year changes in temperature are mirrored by geographical relationships between phenology and regional temperature. For example, mean peak flight date for microlepidoptera is 5.1 days later in the north than in the south of the Netherlands, reflecting a 0.9°C difference in mean annual temperature (Ellis *et al*., 1997). In Britain, 10 out of 29 butterfly species analysed had significantly earlier mean flight dates at warmer lower latitudes, with an average advance of 2.4 days/100 km moved south for these 10 species (equivalent to 6.0 days/1°C) (Roy and Asher, 2003). Insect emergence date also becomes delayed at higher elevations in mountainous regions (e.g. Hill and Hodkinson, 1995; Gutiérrez and Menéndez, 1998; Bird and Hodkinson, 1999; Fielding *et al*., 1999), potentially restricting species to shorter periods of adult activity (Gutiérrez and Menéndez, 1998). In some insects these delays in activity can be avoided by local adaptations at cooler locations, for example in habitat selection for particularly warm microclimates (Thomas, 1993), or in faster growth rates and smaller adult sizes (Nylin and Svard, 1991; Ayres and Scriber, 1994).

3 Mechanisms behind Climate-related Shifts in Distributions and Phenology

3.1 Climate and population size

In addition to showing how increasing temperatures lead to advances in phenology, long-term butterfly monitoring data have shown the relationships between population sizes and weather conditions (e.g. Pollard, 1988; Roy *et al*., 2001). These studies show that the annual population sizes of the

vast majority of British butterflies are positively related to warm dry conditions during the spring and summer of flight, and warm wet conditions during the preceding year. However, the precise relationship depends on the life history of the species concerned. For example, the population sizes of several bivoltine species are most strongly associated with high temperatures in the current spring or summer, providing suitable conditions for larval and pupal development and adult activity. In contrast, hot or dry conditions in the previous year are associated with population declines in species such as ringlet *Aphantopus hyperantus* and speckled wood *P. aegeria*, whose larvae feed on plants growing in moist or partly shaded habitats and may be susceptible to increased drought stress. Similar negative relationships between population size and hot or dry conditions might be expected at the warm margins of species ranges. These year-to-year changes in population size represent the raw material for distributional shifts, with local extinctions occurring where population size declines, and range expansions where population size increases (weather conditions could also affect colonization rate through their effects on dispersal activity, e.g. White and Levin, 1981; Shreeve, 1992). Because of this link, Roy *et al*. (2001) were able to use models relating population size to weather conditions in 1976–1991 to predict historical changes in the abundance of three species in Britain over two centuries, based on historical meteorological and entomological records.

Detailed information on fluctuations in insect population distribution and abundance in Britain has also been provided by the Rothamsted Insect Survey (RIS) (see Conrad *et al*., Chapter 9, this volume). Data from 406 light traps show the pronounced changes in populations of the garden tiger moth *Arctia caja* that have accompanied recent climate change (Conrad *et al*., 2001, 2002, 2003). Population size of *A. caja* decreases in years with high rainfall or temperature in winter and early spring, and in spans of years with high index values for the East Atlantic (EA) teleconnection pattern, an atmospheric circulation system that affects winter weather in western Europe (Conrad *et al*., 2003). Increasing winter temperature, rainfall and EA index values between 1968 and 1998 led to declines in *A. caja* local population density and distribution size, and a shift in its centres of distribution and abundance towards cooler, higher latitudes (Conrad *et al*., 2002). A time lag in the response of species distribution to climate change was observed, with mean local population density falling abruptly between 1983 and 1984, and the proportion of occupied locations declining markedly between 1987 and 1988 (Conrad *et al*., 2001). Increased *A. caja* mortality in warm, wet winters appears to be the cause of its distribution-level decline, but variation in weather systems like the EA teleconnection pattern, the El Niño Southern Oscillation and the North Atlantic Oscillation could lead to changes in insect population dynamics in a variety of ways (Holmgren *et al*., 2001; Ottersen *et al*., 2001). For example, increased rainfall on arid islands in the Gulf of California associated with the 1992–1993 El Niño event led to greatly increased plant productivity, a doubling of insect abundance relative to 1991 and a shift from an insect community composed largely of scavengers and detritivores to one dominated by herbivores (Polis *et al*., 1997).

3.2 Direct effects of climate on growth, survival and fecundity

Temperature is the climatic variable for which there is most evidence of direct effects on insect life history (Bale *et al*., 2002). The temperatures experienced by particular life stages of insects can have important effects on their growth, development, survival and fecundity. Whether climatic changes have a positive or negative effect on population sizes depends on whether the changes take insect life stages nearer to, or further from, the limits of their tolerance, and whether they increase or decrease the synchrony in space or time of insects with interacting species such as host organisms, competitors and natural enemies.

At temperate latitudes, where most insects grow or are active only during warm parts of the year, increasing temperatures often lead to an earlier breaking of winter diapause (Buse and Good, 1996; Miles *et al*., 1997; Masters *et al*., 1998; Fielding *et al*., 1999), although in many species this process is at least partly under photoperiodic control (Hill and Hodkinson, 1996; Bradshaw and Holzapfel, 2001). Faster and earlier growth may allow multivoltine temperate insects with permanently available food supplies to increase population size by increasing their annual number of generations (Roy and Sparks, 2000). However, species that use only periodically available resources may not be able to increase activity periods or population sizes if there is no change in the temporal availability of food. Subtle differences between the cues involved in phenology at different trophic levels could lead to asynchrony between the emergence of larvae and the availability of their food. For herbivorous insects that feed on plant tissues whose palatability or nutrient richness changes over time, synchrony of larval emergence with plant growth can be critical (Feeny, 1970; Hill and Hodkinson, 1995; Hill *et al*., 1998; Bale *et al*., 2002; Hodkinson, 2005). Tree life cycles have only advanced by an average of 3 days accompanying recent climate change, compared with 5 days per decade for invertebrate life cycles (Root *et al*., 2003), showing the potential for mismatches in the phenology of insects and arboreal host plants. For example, recent increases in mean winter temperature without an accompanying decline in the number of frost days have reduced synchrony between egg hatching by the winter moth *Operophtera brumata* and budburst by its host *Quercus robur* (Visser and Hollemann, 2001).

Changes in growth rate can also affect the level of synchrony between specialist insect parasitoids and their hosts. Synchrony between the Glanville fritillary butterfly *Melitaea cinxia* and its parasitoid *Cotesia melitaearum* decreases in cool years, because dark-coloured *M. cinxia* larvae increase their development rate by basking, whereas white, immobile *C. melitaearum* cocoons develop slowly in shaded microclimates. As a result, *M. cinxia* larvae pupate before adult parasitoid emergence and egg laying in cool years, reducing *C. melitaearum* population size, increasing its risk of local extinction and reducing its colonization rate (Van Nouhuys and Lei, 2004). Phenological change by insects can in turn affect levels of predation by other taxa at higher trophic levels: for example, great tits *Parus major* in the Netherlands have not advanced their egg-laying date to keep pace with changes to the temporal availability of caterpillars, their major food source (Visser *et al*., 1998).

Relative synchrony in the growth of insects and their larval host plants can also determine the limits to species' geographic ranges, if at high temperatures host plants grow too quickly for insect exploitation of palatable tissues, or at low temperatures plants grow too slowly for insect development (Maclean, 1983; Bale *et al*., 2002). At the local scale, host plants senesce before larvae of Edith's checkerspot butterfly *E. editha* reach summer diapause on south-facing slopes in hot years, whereas larval development is too slow on north-facing slopes during cool years (Weiss *et al*., 1988). At the scale of species ranges, willow psyllids *Cacopsylla* spp. have a narrower range of larval host plant species and exploit a narrower range of plant tissues at the extremes of their distributional range because of the constraints of maintaining synchrony between larval and host development (Hodkinson, 1997; Hill *et al*., 1998).

In addition to affecting the rate of growth, temperature directly influences mortality, with reduced survivorship towards both lower and upper thermal tolerances (Ratte, 1985). For example, the proportion of individuals developing to adulthood in the peacock *Inachis io* and comma *P. c-album* butterflies was >60% at temperatures of 15–30°C, but at temperatures of 9°C and 34°C, respectively 0% and 20–40% of individuals reached maturity (Bryant *et al*., 1997). The upper latitudinal range margins of these species correspond to the 15°C July isotherm perhaps as a consequence of their requirements for sufficiently warm temperatures for summer larval survival and development.

Changes to ambient temperature, moisture availability and atmospheric CO_2 can have important effects on insect growth and larval host plant quality. Elevated CO_2 concentrations lead to reduced nitrogen levels and increased C/N ratios in leaves, and hence reduced insect performance (growth rate, weight gain and survival) (Coviella and Trumble, 1999; Zvereva and Kozlov, 2006). Most experimental studies show a positive effect of temperature on insect herbivore performance, such that there is no significant change in performance when CO_2 and temperature are increased together (for a review, see Zvereva and Kozlov, 2006). However, warming does not always mitigate the negative effects of elevated CO_2. For example, increased CO_2 levels do not affect survivorship in the leaf miner *Dialectica scalariella* at low ambient temperatures, because larvae feed for longer to compensate for reduced food quality. But at elevated temperatures development is accelerated and the short-time feeding on poor-quality food reduces survivorship and adult weight (Johns and Hughes, 2002). In a counter-example, increased temperatures at low CO_2 levels cause wilting and premature leaf loss in *Lantana camara*, reducing survivorship of the chrysomelid beetles *Octotoma championi* and *O. scabripennis*. At high temperatures, survival of the beetles is favoured by elevated CO_2 levels, because reduced water stress delays leaf loss (Johns *et al*., 2003). Field-scale climate manipulation experiments show that interactions between the weather and plant biochemistry can exert marked effects on insect population dynamics. For example, the abundance of Auchenorrhyncha (Hemiptera) increased with summer rainfall and vegetation cover, but showed no decrease under drought conditions, even though vegetation cover became sparser, probably because drought-stressed foliage had a higher nutritional quality (Masters

et al., 1998). Food web models suggest that climate-induced changes to plant productivity and host plant quality could result in smaller and more variable herbivore population sizes, leading to weaker interactions between trophic levels (Emmerson *et al*., 2004). For aphids, whose physiology has been studied in detail, the population dynamic effects of climate change have been modelled, taking account of climatic variables, CO_2 levels and interacting species (Hoover and Newman, 2004; Newman, 2004, 2005). These models predict that, under realistic CO_2 emission scenarios, changes to temperature and rainfall are the most important drivers of aphid population dynamics; but the prediction of the effects of higher emissions scenarios will require the modelling of sometimes complex interactions among variables (Newman, 2005).

For many temperate insects, mortality during the overwintering period may have important effects on population dynamics and the geographical limits to species distributions (Virtanen *et al*., 1998; Bale *et al*., 2002; Turnock and Fields, 2005). The minimum temperatures that can be experienced by overwintering stages may set the upper latitudinal limits to species ranges, and recent increases in winter temperatures have led to northward range expansions by increasing overwintering survival in insects such as the southern green stink bug *Nezara viridula* (Musolin and Numata, 2003) and the sachem skipper butterfly *Atalopedes campestris* (Crozier, 2003, 2004a,b). In contrast, low temperatures may be beneficial for species that spend winter in an inactive diapause, with reduced metabolic rate in cooler microhabitats associated with increased survival and fecundity in the goldenrod gall fly *Eurosta solidaginis* (Irwin and Lee, 2000, 2003). Survival by overwintering adults of the peacock butterfly *I. io* is affected both by temperature and moisture conditions, with greatly reduced survival at 10°C compared with 2°C, and in wet versus dry conditions (Pullin and Bale, 1989). The location of *I. io*'s southern geographic range margin near the 10°C January isotherm may result from its requirements for cold overwintering conditions (Bryant *et al*., 1997).

The increasing severity or frequency of extreme climatic events such as droughts or unseasonal storms may be as important for long-term population survival as the effects of average changes to climatic conditions (Easterling *et al*., 2000; Parmesan *et al*., 2000). The potential for extreme events to impact on population dynamics is greatest in populations that are highly localized in space, or that breed in homogeneous habitats and are therefore uniformly exposed to the extreme conditions. Cold, wet weather at overwintering aggregations of the monarch butterfly *Danaus plexippus* can dramatically increase mortality (Oberhauser and Peterson, 2003). Two Californian populations of the butterfly *Euphydryas editha* went extinct in association with increased variability in precipitation, which reduced the temporal overlap between butterfly larvae and their host plants (McLaughlin *et al*., 2002a). Of the two populations that were studied, population variation was greater and extinction was faster at the large, flat site than the smaller, more topographically variable site, where the topographic variation acted as a buffer against environmental extremes by increasing the annual period of host plant availability

(McLaughlin *et al*., 2002b). Extreme events at individual locations are likely to affect species differently depending on their microclimatic associations, physiological tolerances and their position in the geographic range, which may potentially lead to changes in community composition. For example, drought conditions in Britain in 1995 and 1996 led to increases in the population sizes of southerly distributed butterfly species, but decreases in the abundance of carabid beetles that favoured low temperatures and wet soils (Morecroft *et al*., 2002).

Temperature can also influence fecundity, through its effects on adult insect activity and the availability of suitable microhabitats for egg laying. The silver-spotted skipper butterfly *Hesperia comma* reaches its northern range margin in Britain, where it has been historically restricted to the hottest microclimates, laying its eggs on small tufts (<5 cm) of the larval host plant *Festuca ovina* in chalk grassland in southern England (Thomas *et al*., 1986). This thermophilic habitat restriction was responsible for a pronounced decline in the British distribution of *H. comma* from the 1950s to the 1980s, when the abandonment of low-intensity livestock grazing and a rabbit decline caused by myxomatosis led to unsuitable tall vegetation across most sites in its former range. By 1982, the species was restricted to less than 70 refuge populations in England, nearly all of them on south-facing grassland with thin soils and a large amount of bare ground (Thomas *et al*., 1986). However, following a recovery in rabbit populations and conservation grazing management in and around the refuge sites, *H. comma* spread its regional distribution and by 2000 had over 250 populations in England, many of them re-colonizations of formerly occupied localities (Thomas and Jones, 1993; Davies *et al*., 2005). This range expansion was achieved partly as a result of improving habitat conditions in the refuge populations and surrounding sites, but is also related to warmer climates increasing fecundity. Field observation and experiments show that *H. comma* females lay a larger number of eggs in warmer conditions, and that the microhabitats used for egg laying change depending on ambient temperature: at low ambient temperatures, eggs are laid in particularly warm microhabitats, but at higher temperatures eggs are laid on plants growing in conditions that are no warmer, or even cooler, than ambient conditions (Fig. 11.2a) (Davies *et al*., 2006). Between 1982 and 2001 (during which time local mean August temperature rose by 2°C), the typical microhabitat used for egg laying by *H. comma* changed (Fig. 11.2b), with the optimum proportion of bare ground declining from 41% to 21%, shown by logistic regression modelling of the probability of egg occurrence based on quadrats performed in the same locations 20 years apart. Most habitat patches in the networks of chalk grassland where *H. comma* occurs in England have a percentage cover of bare ground much closer to the new optimum for egg laying. As a result the species has been able to exploit larger areas of habitat in each grassland patch and colonize some habitat patches that would have been unsuitable under its earlier, more restrictive habitat requirements (including many sites on east, west and even north-facing slopes; Thomas *et al*., 2001). Thus, climate warming has increased the availability of thermally suitable habitat for *H. comma* at the cool, northern edge of the species range, leading

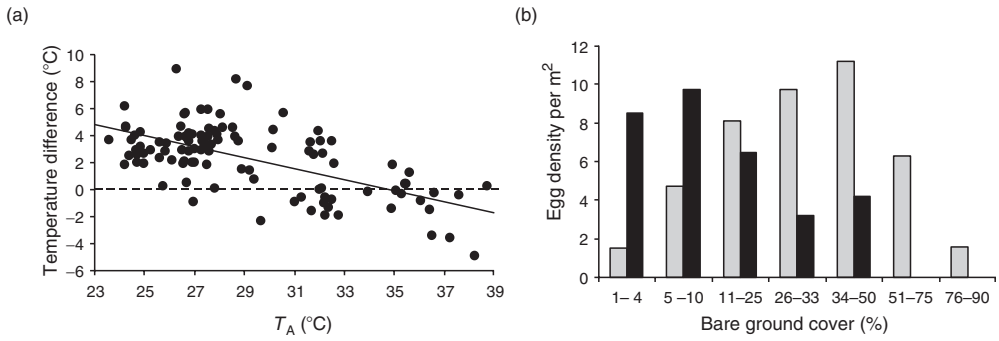

Fig. 11.2. Changing microhabitat choice in the butterfly *Hesperia comma*, associated with warming temperatures. (a) The temperature difference between sites selected for egg laying and ambient temperature (T_A) declined at increasing ambient temperature: Temperature difference = [AU1] $-0.41\ (\pm 0.05) \times T_A + 14.16\ (\pm 1.51)$; $R^2 = 0.38$, $F_{1.103} = 63.12$, $P < 0.001$. (b) The density of eggs against percentage cover bare ground in 25 × 25 cm quadrats repeated at the same location in 1982 (grey bars) and 2001 (black bars). In 1982, eggs were associated with higher percentage cover bare ground (hotter microclimates) than in 2001. (Reproduced from Davies *et al*., 2006, with permission from Blackwell Publishing.)

to increases in: (i) egg-laying rate; (ii) the effective area or population carrying capacity of habitat patches; and (iii) the number of habitat patches in the landscape that are available for colonization. Now that *H. comma* lays eggs in a wider variety of microhabitats, its population dynamics are also likely to be buffered against environmental variation: studies on butterflies (Sutcliffe *et al*., 1997; McLaughlin *et al*., 2002b) and the bush cricket *Metrioptera bicolor* (Kindvall, 1996) show that habitat heterogeneity can reduce the risk of local population extinction from fluctuating weather conditions (see Section 5).

3.3 Biotic interactions

In our discussion of the direct effects of climate on insects we have already considered some important interactions between climate, insects and their host organisms. Future distributions of insects will be constrained by the future distributions of their specific host species, or by climates in which they are phenologically synchronized with their food supplies (Hodkinson, 1999). Changes in host plant use across an insect species' range (e.g. Hodkinson, 1997) could interact with changing climates, with consequences for rates or patterns of range shifts. For example, recent northward range expansions in Britain by the brown argus *A. agestis* and comma *P. c-album* butterflies appear to have been facilitated by shifts in diet to incorporate increased use of widespread larval host plants (Thomas *et al*., 2001; B. Braschler and J.K. [AU2] Hill, unpublished data).

Interacting competitors, predators, parasitoids and pathogens could also affect the responses of species to climate change. A general effect of warmer

temperatures could be increased growth rates, leading to reductions in mortality because of reduced exposure times of larvae to predation or parasitism (Bernays, 1997). The presence of particular interacting species can also influence the relationships between climatic conditions and species population size. For example, the fruit flies *Drosophila melanogaster*, *D. simulans* and *D. subobscura* coexist in the wild in southern Europe. Using laboratory microcosms, Davis *et al*. (1998) showed changes to the distribution and abundance of the three competing flies along a temperature cline of 10–25°C, depending on whether the species were alone or in the presence of their competitors. Population density of *D. subobscura* was reduced at temperatures of 15–20°C by the presence of *D. simulans*, whose population density was reduced at 10–15°C by *D. subobscura*; further addition of *D. melanogaster* caused the disappearance of *D. subobscura* at 25°C, and of *D. simulans* at 10°C. Addition of a parasitoid wasp *Leptopilina boulardi* led to further changes in abundance and distribution, with increases in population density of *D. melanogaster* at 20–25°C and of *D. subobscura* at 10–15°C, because of reductions in competitor density caused by the parasitoid. A 5°C increase in temperature, producing a cline of 15–30°C, led to the disappearance of *D. subobscura* from the 25°C treatment because of immigration by *D. melanogaster* and *D. simulans* from the 30°C cage, where the latter two species had high population density. In the same 15–30°C cline, there was an unexpected increase in *D. subobscura* abundance at 15°C.

The overall effect of species interactions may be to reduce the predictability of ecological responses to climate change, particularly when abundance and distributions are set by a few strong interactions (as opposed to a more diffuse pattern of interactions with many other species). Because species shift their distributions individualistically when climates change (e.g. Coope, 2004), shifting biotic interactions could alter the relationships of species population abundance and distribution with climate (Davis *et al*., 1998). However, the importance of changing biotic interactions in predicting responses to climate change remains uncertain. Levels of predation or parasitism decline towards the upper latitudinal or elevational margins of species ranges, and if the ecophysiological limitations of species and their natural enemies are known, we might be able to predict the effects of climate change on the future ranges of both (Hodkinson, 1999). The problem with this approach is that species distributions and abundances change at different rates, depending on their dispersal ability and original abundance and distribution sizes, and this may make transient dynamics particularly difficult to predict. Time lags before natural enemies tracked the expanding ranges of herbivorous insects may have led to the increases in insect herbivory indicated by fossil plants following periods of climate warming (Wilf and Labandeira, 1999). The climatic or biotic limiting factors for particular interacting species may also be difficult to predict. For example, after increases in plant productivity associated with heavy rains in desert islands in the Gulf of California, spider densities doubled in 1992 in response to increased insect prey, but then were greatly reduced in 1993 because of parasitism by wasps whose populations increased because of increased nectar and pollen resources (Polis *et al*., 1998).

3.4 Interactions of climate change with habitat loss and fragmentation

Evidence for 20th-century changes shows that many species have not been able to shift their distributions to track suitable climate space. For example, 46 non-migratory species of butterfly reach their upper latitudinal range margins in Britain, and recent increases in summer temperatures should have increased both local population densities and distribution sizes for these species (Roy *et al*., 2001). However, between distribution surveys in 1970–1982 and 1995–1999, most butterfly species showed declines both in local population abundance and distribution size (Warren *et al*., 2001). In particular, the distributions of sedentary, habitat specialists declined (24 out of 26 species), whereas half of the mobile, habitat generalist butterfly species expanded their range (9 out of 18 species). Even for relatively dispersive butterfly species, rates of range expansion into suitable climate space are constrained by the availability of suitable habitat (Hill *et al*., 1999b, 2001).

One consequence of the differential abilities of species to track changing climates across anthropogenically altered landscapes could be a shift in the composition of ecological communities, away from habitat specialist and sedentary species towards wide-ranging, generalist species (Tilman *et al*., 1994; Warren *et al*., 2001; Menéndez *et al*., 2006). The restructuring of ecological communities could have untold consequences for a wide range of ecological and evolutionary processes, particularly relating to ecosystem functioning and the effects of biotic interactions on species' responses to climate change (see Section 3.2.).

3.5 Interactions between phenological and temperature change

The consequences of phenological advancement have generally been considered in terms of a possible disruption of synchrony with host species, and a possible lengthening of the annual adult activity period (e.g. Roy and Sparks, 2000). A hitherto overlooked effect of phenological advancement is its effect on the temperatures that particular stages of insect life cycles experience. Whilst average annual temperatures have risen, certain stages of species' life cycles may encounter either cooler or warmer conditions as a result of the interaction between phenology shifts and changes in mean temperature. To illustrate this point, we investigated the net change in temperature that might have been experienced based on a combination of temperature changes and recent phenological advancement by adults of two univoltine butterfly species in the UK: the orange tip *Anthocharis cardamines*, which flies in spring, and the silver-spotted skipper *H. comma*, which flies in late summer. Peak flight date for each year between 1985 and 2004 (the longest period that had continuous records for both species from transects of the British Butterfly Monitoring Scheme) was calculated for each transect where at least four individuals were counted for either species. Change in phenology over time was calculated by the linear regression of peak date against year, giving advances

of 5.5 days per decade for *A. cardamines* (peak date = −0.55 (± 0.09) *X* year + 1234.07 (± 182.73); $R^2 = 0.08$, $F_{1.432} = 36.66$, $P < 0.001$) and 4.7 days per decade for *H. comma* (peak date = −0.47 (± 0.11) *X* year + 1168.73 (± 223.12); $R^2 = 0.22$, $F_{1.62} = 17.82$, $P < 0.001$). At the nearest meteorological station (Mickleham) to the site where the *H. comma* egg-laying experiments were carried out (see Section 3.2), mean daily air temperature records had increased for given calendar dates between 1985 and 2004: by 1.1°C during the flight period of *A. cardamines* (mean first sighting date 18 April, mean last sighting 1 June) and by 2.0°C in *H. comma*'s flight period (1 August to 4 September). However, the concurrent advance in flight date of 11 days for *A. cardamines* led to its emergence earlier in spring, which would on average be 1.5°C cooler (the 'phenological shift', based on differences between dates during the flight period between 1985 and 2004), so that the temperature experienced by adult *A. cardamines* became cooler by 0.4°C (Fig. 11.3a). In contrast, the 9-day advance in *H. comma*'s flight period towards earlier August led to a 'phenological shift' in temperature of + 0.8°C because adults were now flying at a hotter time of the year. The phenological shift combined with the 2°C increase in August temperatures would lead to a net change of 2.8°C in the temperatures experienced by *H. comma* adults (Fig. 11.3b), potentially having a major effect on flight activity and habitat choice by the butterflies. Because *H. comma* egg-laying rate is positively correlated with temperature in Britain, this is likely to have resulted in a substantial increase in realized fecundity (Davies *et al.*, 2006).

We also estimated the net changes in temperature that would be experienced at different times of the year, based on changes to the Central England temperature between 1961 and 2000 (Manley, 1974; Parker *et al.*, 1992) and an average advance of 2.3 days per decade of phenological events (Parmesan and Yohe, 2003) (Fig. 11.3c). In agreement with the results presented based on local meteorological data and the flight periods of *A. cardamines* and *H. comma*, these results suggest that species or life stages that are active at dates from July until March will have experienced net increases in temperature, because of a synergy between year-to-year warming and phenological advance. In contrast, those parts of species life cycles that are active between April and June may have experienced a net reduction in temperature, even though spring temperatures are increasing. The reduction of net temperatures through late spring/early summer and exaggerated warming during the rest of the year may have repercussions for temperature-dependent activities of individual species. One consequence might be an increased effect of climate change on species whose most climate-sensitive stages are active at times of year experiencing large net changes in temperature. However, temperature will affect all stages of an insect life cycle, including diapause, so it is more satisfactory to consider the effects of net predicted changes on all individual stages. One concern is that there may be mismatches between the habitats selected, for instance, by egg-laying adults and those required by larvae, if microhabitat selection at different times of the year is based on the microclimates experienced (e.g. Roy and Thomas, 2003).

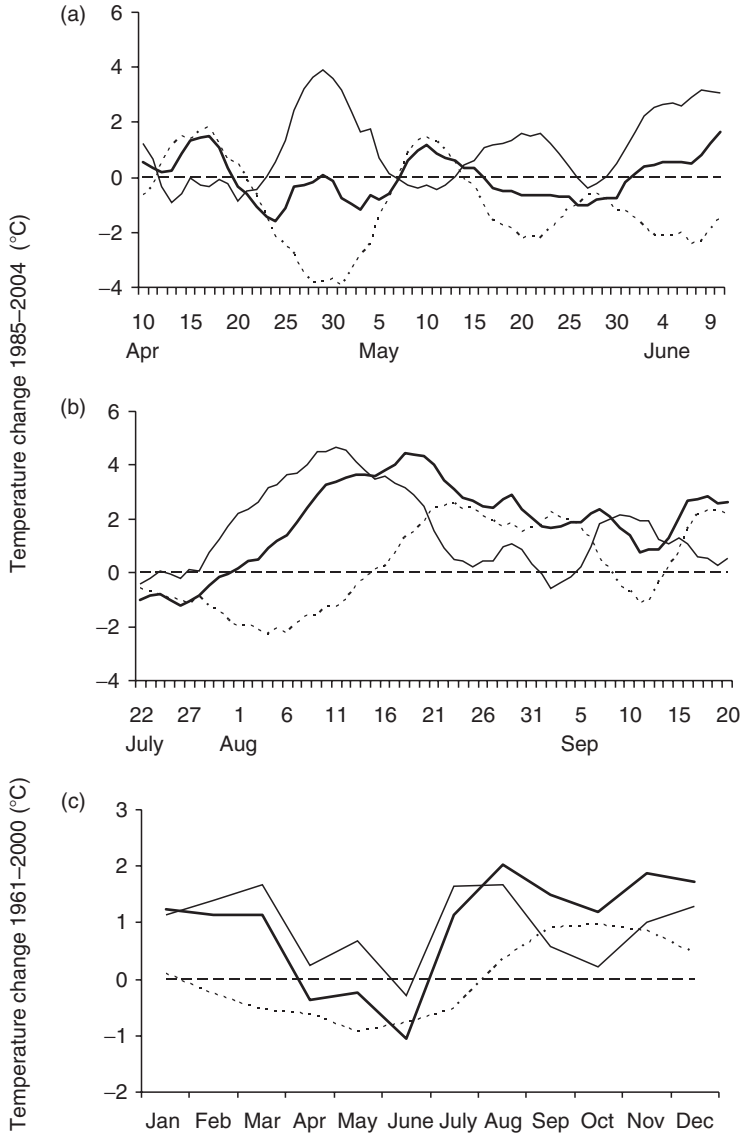

Fig. 11.3. Estimated net change in temperature experienced at different times of year as a result of climate warming and phenological advancement. Net change = thick continuous line; climate change = thin continuous line; direct effect of phenological advance = dotted line. (a) and (b) show week-long running mean changes based on temperature records from 1985 to 2004 at Mickleham in south-east England and phenological change in flight period over the same time for the butterflies: (a) *Anthocharis cardamines*, a spring-flying species; and (b) *Hesperia comma*, a late summer species. (c) shows estimated average change per activity month based on an 11-day advancement and changes in the Central England Temperature Series between 1961 and 2000. See Section 3.4 for details.

3.6 Adaptive responses

Most palaeological evidence suggests that insects have shifted their distributions to track suitable climates during periods of Quaternary climate change (the last 2 million years), rather than adapting *in situ* to changing conditions (Coope, 2004). Nevertheless, insects often have large population sizes and short generation times, and changes in selection may occur rapidly during periods of rapid climate change (Thomas, 2005). There may be selection for phenotypes that favour rapid expansion at range margins where climatic conditions improve, such as those associated with dispersal or the exploitation of novel or widespread resources. Contemporary evolutionary responses at expanding range margins include selection for dispersive forms of butterflies (Hill *et al*., 1999a,c), ground beetles (Niemela and Spence, 1991) and bush crickets (Thomas *et al*., 2001; Simmons and Thomas, 2004), and for increased egg laying on a widespread host plant relative to a more restricted former host by the brown argus butterfly *A. agestis* (Thomas *et al*., 2001). These adaptations increase the rate at which species are able to track shifting suitable climate space, but once populations have been established, there may be a return to selection against dispersive forms, which may be associated with reduced fecundity (Hughes *et al*., 2003; Simmons and Thomas, 2004). Therefore, forms adapted to range expansion may be favoured for a relatively short period and not readily detected by the fossil record.

The potential for adaptation during changing climates is dependent on the reservoir of genetic variation within populations of species. Many species show adaptations to the local climates experienced in different parts of their geographical range, for example in terms of size, growth rate, diapause induction or the range of plastic responses that can be elicited from individual genotypes (Ayres and Scriber, 1994; Nylin and Gotthard, 1998; Berner *et al*., 2004). There are differences in preferred oviposition temperature, tolerance of drought and high temperatures, as well as longevity patterns for populations of the fruit fly *D. melanogaster* between hot, dry south-facing slopes and cooler, moister north-facing slopes in close proximity in Israel (Korol *et al*., 2000). Species often show adaptive local variation in the day-length reduction that is required to induce winter diapause, with longer day lengths sufficient to induce diapause at locations, such as higher latitudes or elevations, where conditions deteriorate earlier in the year (e.g. Roff, 1980; Pullin, 1986; Gomi, 1997). The genetically controlled critical photoperiod for winter diapause induction in populations of the pitcher plant mosquito *Wyeomyia smithii* declined between 1972 and 1996, leading to later cessation of larval activity in conjunction with increasingly warm summers and later onset of autumn conditions (Bradshaw and Holzapfel, 2001).

Despite widespread genotypic and phenotypic variation across the geographical ranges of species, the ability of populations to adapt to new conditions will depend on their location in the current range. Populations at expanding range margins may be able to adapt relatively rapidly because of gene flow from the core of the species range. However, at the rear or trailing edge of a species distribution, the new prevailing conditions are less likely to have been

experienced by populations of the species during its evolutionary past, such that the potential for pre-existing genetic variation to allow adaptation is much lower (Thomas, 2005). In addition, deteriorating conditions at the rear edge of species distributions are likely to reduce the extent of suitable habitat (e.g. Wilson *et al*., 2005), leading to smaller, more isolated populations that contain reduced genetic variation and are prone to effects of inbreeding (Saccheri *et al*., 1998). Species ranges have undergone successive shifts towards and away from the poles associated with Quaternary periods of warming and cooling: during these alternating shifts, isolated rear-edge populations may have developed local adaptations that were 'swallowed up' by gene flow from the core of the range when climatic conditions reversed (Coope, 2004). As a result, the greatest reservoir of genetic diversity occurs in parts of species ranges that have remained occupied during both glacial and interglacial periods (Hewitt, 2004; Schmitt and Hewitt, 2004). During current, interglacial conditions, this zone of greatest genetic diversity is located near the lower latitudinal margin of most species, where climate-related extinctions could represent a significant loss of future potentially adaptive variation (Hampe and Petit, 2005).

4 Modelling Future Effects of Climate Change

Geographic-scale correlations of species distributions with particular climatic conditions can be used to infer climatic constraints on species ranges, and thus to model 'bioclimate envelopes' for individual species (Pearson and Dawson, 2003). Climate envelope models have been constructed for a number of insects, allowing the prediction of the future locations of suitable climates based on their current climatic associations and realistic scenarios of climatic change (e.g. Hill *et al*., 1999b, 2002; Beaumont and Hughes, 2002; Oberhauser and Peterson, 2003; Luoto *et al*., 2005). Climate envelope models can be constructed using variables that have a priori associations with insect distributions, for example, annual cumulative temperature above a threshold level (that affects rates of growth and development), minimum winter temperatures (that affect overwintering survival) and moisture availability (that affects primary production) (e.g. Hill *et al*., 2002; Luoto *et al*., 2005).

Climate envelope models fit current species distributions well, both at upper and lower latitudinal range margins (Hill *et al*., 2002), and appear to perform well for a variety of taxa (Huntley *et al*., 2004). The models are relatively accurate for species whose distributions are contiguous, with the bounds likely to be set by climatic limitations either on the species itself or on some vital interacting species, such as a larval host plant. Models do not perform well for species that have widespread but scattered distributions, where habitat restrictions and/or local colonization–extinction dynamics may dominate distribution patterns within the climatically suitable range (Luoto *et al*., 2005). Factors such as biotic interactions, local topographical variation and local evolutionary adaptation could also lead to discrepancies between observed distributions and those modelled based on coarse-scale climatic associations (e.g. Davis *et al*., 1998; Hill *et al*., 1999, 2002). [AU3]

Nevertheless, modelling future areas of suitable climate space for species, based on their current associations and future scenarios of climate change, allows very general conclusions to be drawn about the likely effects of climate change on species ranges, relative vulnerability of particular groups of species and relative effects of different scenarios of climate change or carbon emission levels (e.g. Beaumont and Hughes, 2002; Hill *et al*., 2002; Peterson *et al*., 2002; Thomas, C.D. *et al*., 2004). Modelling the current and future European distributions of 35 geographically widespread species of butterflies based on their current climate associations suggested that distribution sizes would not change significantly in the 21st century, as long as there were no geographical constraints to range shifts and species ranges were able to track suitable climate space perfectly (Hill *et al*., 2002). However, if the 30 out of 35 species that have not shifted their distributions in conjunction with recent climate change were considered only to survive in areas of overlap between current and future favourable climates, the average predicted change in distribution size would be a 31% decline, and the five modelled species that were restricted to high latitudes in Britain and Europe would have an average predicted decline of 65% (Hill *et al*., 2002). The climatically suitable ranges for 70 out of 77 Australian endemic butterfly species are predicted to decrease in size based on modelled climates in 2050, with areas of overlap of current and future distributions ranging from 63% to only 22% under conservative and more extreme scenarios of climate change (Beaumont and Hughes, 2002). It is evident that the distributions of species that are currently restricted to localized areas such as mountain ranges or islands may show little geographical overlap with locations that are predicted to be climatically suitable in the future. Species that have very narrow climatic tolerances and associated restricted geographical distributions will not be able to survive climate change, unless their populations can adapt to changing conditions.

The task of predicting future ranges is complicated by the dependence of most species on interacting host species, whose future distribution size or overlap with future modelled climate space for a species may also change. For example, overwintering sites for the monarch butterfly *D. plexippus* in Mexico are located in oyamel fir *Abies religiosa* forests that are characterized by cool, dry conditions between November and March. Survival at overwintering sites is a major determinant of annual abundance, and climate modelling suggests that unfavourable cold or wet conditions will prevail in 30 years time across the distribution of *A. religiosa* (Oberhauser and Peterson, 2003). Thus, although the migratory butterfly *D. plexippus* might itself have sufficient mobility to track changing climates, the geographical isolation of its overwintering habitat may prevent it from doing so. Models that include the effects of climate change both on the future distributions of focal species and their hosts may give increasingly realistic results. However, these models are likely to increase estimates of decline unless climate change allows the exploitation of novel hosts (e.g. Thomas *et al*., 2001).

Most studies that have modelled the effects of climate on insects have taken advantage of the detailed information that is available on the distributions, habitat requirements and population dynamics of northern temperate

taxa. The few lower latitude or southern hemisphere exceptions have usually modelled the responses of relatively well-known groups such as the Lepidoptera (Beaumont and Hughes, 2002; Erasmus *et al*., 2002; Oberhauser and Peterson, 2003). Models for the effects of climate change on the huge diversity of insect taxa at tropical latitudes are hampered by a lack of information even of the basic biology of many species (see Lewis and Basset, Chapter 2, this volume). Latitudinal gradients in species richness represent one potential source of information about the potential effects of climate change on biodiversity at lower latitudes. Species richness in the tropics, subtropics and warm temperate zones is closely related to water availability, suggesting that any increase in temperature would need to be accompanied by increasing rainfall to avoid declines in species richness (Hawkins *et al*., 2003).

One possible approach to estimate the vulnerability of taxa to climate change in poorly studied regions is to focus on the climate and habitat associations of species or morphospecies within an insect community. Andrew and Hughes (2004, 2005) sampled the Coleoptera and Hemiptera feeding on *Acacia falcata* at four latitudes from 26°7′S to 35°40′S on the east coast of Australia, and classified the species into four functional groups (named here in italics). *Cosmopolitan* species, which were found at more than one of the sample latitudes and on more than one host plant species, should be resilient to climate change. *Generalist feeders*, which were found only at one latitude but on more than one host plant, may be able to move their climate envelope by exploiting different hosts. The future distributions of *climate generalists*, which were only found on *A. falcata* but at more than one latitude, may be constrained more by their host plant than by climate change. *Specialists*, restricted to *A. falcata* at only one latitude, are expected to be most vulnerable to climate change, and constituted the most diverse group (50% of Coleoptera and 38% of Hemiptera). Many tropical insect species appear to be very rare, with high host plant specificity, localized distributions or low population density (Price *et al*., 1995; Novotný and Basset, 2000) and may therefore struggle to respond to climate change. Well-designed taxonomic inventories such as those of Andrew and Hughes (2004, 2005) could be a valuable source of information about the effects of climate change on insect communities at tropical latitudes.

5 Climate Change and Insect Conservation

Evidence shows that insect species are shifting their ranges to accompany recent climate warming as they did in prehistoric periods of climate change (Wilf and Labandeira, 1999; Coope, 2004; Hewitt, 2004). A major challenge for conservation is to prevent species disappearing from climatically deteriorating parts of their range before they can colonize regions or habitats that become suitable. This challenge is compounded by additional drivers such as land use change and exotic species introductions that already threaten many species with extinction, and whose effects need to be borne in mind when designing conservation strategies (Sala *et al*., 2000; Gabriel *et al*., 2001;

Thomas, J.A. *et al*., 2004; Balmford and Bond, 2005). The foregoing discussion shows that species are likely to respond to climate change in individualistic ways, leading to sometimes unpredictable changes in distribution and abundance patterns, phenology and interactions between species. Conservation programmes may need to be similarly flexible and dynamic as a result, and may require modification to explicitly include the effects of climate change (Hannah *et al*., 2002a,b; Hulme, 2005). We draw four general conclusions concerning insect conservation in a changing climate:

1. Climate change disproportionately threatens species with small or isolated populations or distribution sizes, narrow habitat requirements (or narrow distributions of resources in space or time) and poor dispersal abilities. These factors increase the likelihood that climate variation will result in declines in population size and local extinctions, and reduce the ability of species to exploit novel resources or colonize climatically favourable locations. It is evident that the same characteristics of species that make them particularly vulnerable to climate change also place them at risk from other anthropogenic effects such as habitat loss and fragmentation (e.g. Travis, 2003; Henle *et al*., 2004; Kotiaho *et al*., 2005). Therefore, climate change is likely to increase the vulnerability of most species that were already threatened.

2. Priority conservation management may be required in habitats or regions whose biodiversity is particularly sensitive to the effects of climate change. These regions or habitats can be identified by the modelling of species or biome responses to climate change (e.g. Hannah *et al*., 2002a). At international scales, centres of endemism or biodiversity hotspots represent concentrations of species that are especially vulnerable to changes both in land use and climate (Myers *et al*., 2000). High latitudes and elevations will experience the greatest changes in temperature, potentially shifting the suitable climate space for species to locations far outside their current ranges. Montane areas will be particularly vulnerable because they support a disproportionate number of rare or endemic species (e.g. Van Swaay and Warren, 1999; Williams *et al*., 2003), and because they often represent the lower latitudinal margins of species ranges, which are especially vulnerable to climate warming (Wilson *et al*., 2005) and which may be important reservoirs of genetic variability (Hampe and Petit, 2004). Conversely, mountainous areas may present opportunities for conservation, since: (i) they often retain comparatively intact habitats relative to lowland landscapes; (ii) steep elevational gradients may allow species ranges to track changing climates more quickly and over smaller distances than in the lowlands; and (iii) small-scale topographical variation may allow survival and adaptation in localized refugia. Minimizing the other threats to species in these regions may increase the likelihood that they will survive climate change.

3. At regional scales, landscape-scale habitat management of reserve networks and the wider environment will be important both to maintain current populations of species and to increase their likelihood of colonizing locations or habitats that become more favourable. Rates of range expansion by the butterfly *H. comma* in England were increased because grassland

management in agri-environment schemes increased the area and connectivity of habitat at a landscape scale (Davies *et al*., 2005). Climate-related changes in the habitat associations of *H. comma* meant that it was able to colonize many areas of grassland that would earlier not have been defined as ideal habitat for the species (Davies *et al*., 2006). Thus, site protection or management may benefit species that are present not only at a site itself but in the surrounding landscape, and an appropriate large-scale approach may be required to identify and manage regions or habitat networks that support a large number of species of conservation priority (e.g. Moilanen *et al*., 2005).

Management of the wider landscape to increase connectivity between populations will be least feasible for very sedentary species whose current distributions are very small or very isolated from locations that are expected to be suitable in the future. In this context, management of remnant networks of natural habitat combined with population translocations could be more cost-effective than the creation of wildlife corridors linking highly modified landscapes (Hulme, 2005). Using approaches such as those described in this chapter to model the locations of suitable climates and habitats could aid in the identification of priority species and regions for introductions. Introductions of insect species into suitable habitats beyond their current range have been successful on a number of occasions (e.g. Menéndez *et al*., 2006). However, the scope of population translocations as a conservation tool may be limited to a relatively small number of flagship species by their cost and requirement for very detailed ecological data. It is essential that translocations do not cause more problems than they solve (e.g. bringing incompatible species into contact with one another).

4. The maintenance of habitat heterogeneity at local and landscape scales may favour species' persistence for two reasons. First, the habitat associations of species change with climate over time (Davies *et al*., 2006) and over their geographic ranges (Thomas, 1993; Thomas *et al*., 1998, 1999). As a result, the habitat conditions or management practices that benefit species may change between seasons (Roy and Thomas, 2003) or years (Kindvall, 1996; Sutcliffe *et al*., 1997) and the provision of a variety of habitat or microhabitat types will allow species to exploit the conditions that are most favoured at a particular time. Careful monitoring may be increasingly necessary to detect the relationships of climate with the population sizes and habitat associations of species, as well as to ensure that habitat is not managed according to outdated prescriptions. Second, habitat heterogeneity could act as a buffer against extreme conditions, allowing populations to survive in some locations or habitats when others become temporarily unfavourable or uninhabitable. Habitats that have greater variation in topography or humidity support more persistent populations than more homogeneous habitats for the butterfly *E. editha* (McLaughlin *et al*., 2002b) and the bush cricket *Metrioptera bicolor* (Kindvall, 1996). At a landscape scale, the use of two different types of habitat allowed a population network of *E. editha* to survive a succession of extreme climatic events (Singer and Thomas, 1996; Thomas *et al*., 1996). All populations breeding in forest clearings went extinct in 1992, after early emergence subjected adults to unfavourable conditions in 1989 (asynchrony with nectar

availability) and 1990 (mortality caused by a snowfall), and spring frosts killed host plants in 1992. However, populations survived in rocky outcrops where butterflies emerged later in the year and host plants were not killed by the 1992 frost. Rocky outcrops had supported lower population densities than forest clearings before the extreme climatic events, showing how locations and habitats that appear suboptimal based on current abundance patterns may be vital for long-term persistence in a changing climate.

The guidelines above can help to inform the adaptive management of biodiversity in the face of global change. However, in order to ensure that climate does not change so markedly that biological change is no longer manageable, conservationists also need to engage in political advocacy for reductions in greenhouse gas emissions (Hannah *et al*., 2002b). Minimizing the amount of warming that takes place (climate change *mitigation*) is a prerequisite for the successful conservation management (*adaptation*) of the world's biodiversity in a changing climate.

6 Conclusions

Climate is an important determinant of the abundance and distribution of species. Species are associated with particular latitudes, elevations or habitats through the effects of climate both on the species themselves and on interacting taxa. For species to survive changing climates, they must either adapt *in situ* to new conditions or shift their distributions in pursuit of more favourable ones. Many insects have large population sizes and short generation times, and their phenology, fecundity, survival, selection and habitat use can respond rapidly to climate change. These changes to insect life history in turn produce rapid changes in abundance and distribution size, but some species fare much better than others, particularly in human-altered landscapes. In conjunction with recent climate change, widespread, generalist species at their cool range margins have expanded their distributions, whereas localized, habitat-specialist species and those at their warm margins have declined. In the face of these rapid changes to species, communities and ecosystems, the onus is placed on conservation to be equally dynamic. Landscape-scale conservation, with habitat heterogeneity providing a buffer against extreme conditions and changes in habitat use by threatened species, is an appropriate strategy to conserve species and to assist their colonization of areas that become more favourable as the climate changes.

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[AU1] Pl confirm if this is multiplication sign or alphabet 'X'.

[AU2] Pl provide year of unpublished data.

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